



# THE BIOLOGICAL BULLETIN

PUBLISHED BY THE MARINE BIOLOGICAL LABORATORY

ELECTRICAL ACTIVITY AND BEHAVIOR IN THE SOLITARY  
HYDROID *CORYMORPHA PALMA*. I. SPONTANEOUS  
ACTIVITY IN WHOLE ANIMALS AND IN  
ISOLATED PARTS

ELDON E. BALL<sup>1</sup>

*Department of Biological Sciences, University of California, Santa Barbara, California 93106*

Even before the advent of electrical recording, cnidarians, with their simple nervous systems and apparently simple behavior, attracted many investigators interested in analyzing the physiological basis of behavior. Following Josephson's (1961b) demonstration that it was possible to record large, spontaneous electrical potentials from hydroids, a number of investigators turned their attention to analysis of the relation between electrical activity and behavior in these organisms with the result that this relationship has now been investigated in *Tubularia* (Josephson and Mackie, 1965; Josephson and Urich, 1969), *Hydra* (Passano and McCullough, 1962, 1963, 1964, 1965; Rushforth 1971; Rushforth and Burke, 1971); *Cordylophora* (Josephson 1961a, 1961b; Mackie, 1968); and *Obelia* (Morin and Cooke, 1971a, 1971b). An association between behavior and at least one type of spontaneous electrical activity was observed in all of these hydroids except *Cordylophora*.

From Parker's (1919) description it appeared that *Corymorpha* could exhibit fairly complex behavior as compared with other hydroids. This description and the conclusion by Parmentier and Case (1973) that there was, at best, an indirect relation between activity and behavior in the closely related hydroid *Tubularia* led to my investigation of the relation between electrical activity and behavior in *Corymorpha palma* Torrey. *Corymorpha* is especially favorable for such an investigation because of its large size and its diminutive perisarc, which usually covers less than a fifth of the stalk.

<sup>1</sup> Present address: Department of Neurobiology, Research School of Biological Sciences, P.O. Box 475, Canberra City, A.C.T., 2601, Australia.

## MATERIALS AND METHODS

Specimens of *Corymorpha palma* Torrey (Fig. 1) were collected using SCUBA at depths of up to fifteen feet in Newport Bay, California. They were maintained in aquaria with either open or recirculating sea water systems at temperatures of 12°–23° C and an illumination cycle of 16 hours light and 8 hours of darkness. *Artemia* nauplii were added to each aquarium every day or two.

Gross morphology of *Corymorpha* was investigated by dissection, while for cellular details tissue was fixed in picroformol, embedded in paraffin, sectioned, and stained with hematoxylin and trisoin. Oxidized methylene blue staining for nerves was done on fresh tissue. Individual cell types were examined following maceration of fresh tissue in Bela Haller's macerating fluid (Gatenby and Painter, 1937).

For electrical recording from a whole animal, *Corymorpha* was placed on sand in the bottom of a culture dish (80 × 100 mm) full of sea water adjusted to 20 ± 1° C by immersion in a water bath. This temperature was maintained during

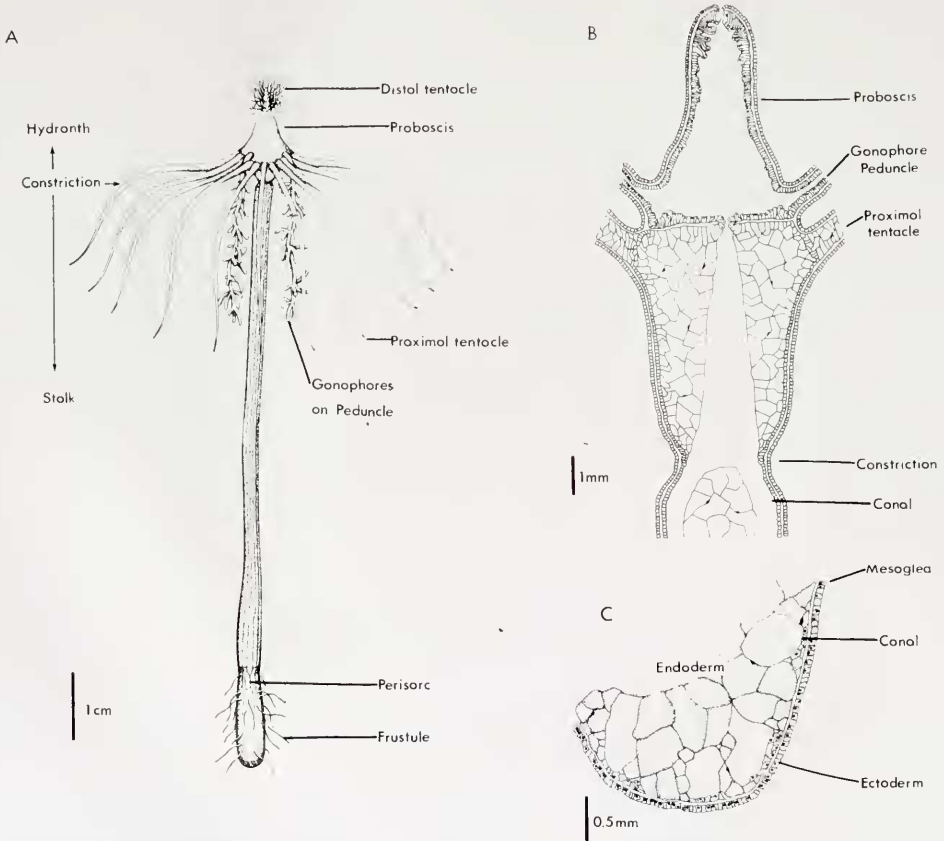


FIGURE 1. *Corymorpha palma* Torrey; (A.) whole animal showing various external features, (B.) longitudinal section of the hydranth, (C.) a partial cross section of the stalk.

recording by a recirculating water-bath or by working in a temperature-controlled room. Sand, which is held in place by the frustules, normally surrounds the bases of the animals, allowing them to be moved without too much disturbance and aiding them in regaining their normal upright stance. A 10–30 minute recovery period was allowed following the transfer of an animal to the culture dish. During this period the animal reassumed the upright posture normally seen in nature.

Electrical recording was done using suction electrodes made by drawing out flexible "Tygon" tubing (i.d. 0.625 mm) to a tip orifice in the range of 50–200  $\mu\text{m}$ , as appropriate to record from the particular part of the animal which was under study. The indifferent electrode was a platinum-iridium wire in the bath. Electrical activity was monitored on a Tektronix 502A oscilloscope and recorded on a Beckman RB Dynograph after amplification with Grass P511 AC preamplifiers.

Excision experiments were performed on animals standing on sand in a culture dish. The normal pattern of electrical activity was first established and then one or more excisions were performed. *Corymorpha* can readily be sectioned at the neck and at the base of the proximal tentacles, making it possible to record from the following parts in various combinations: isolated proximal tentacles, isolated hydranth, and isolated stalk. Recordings were also made from excised gonophores and excised distal tentacles, but these were removed before recording was begun.

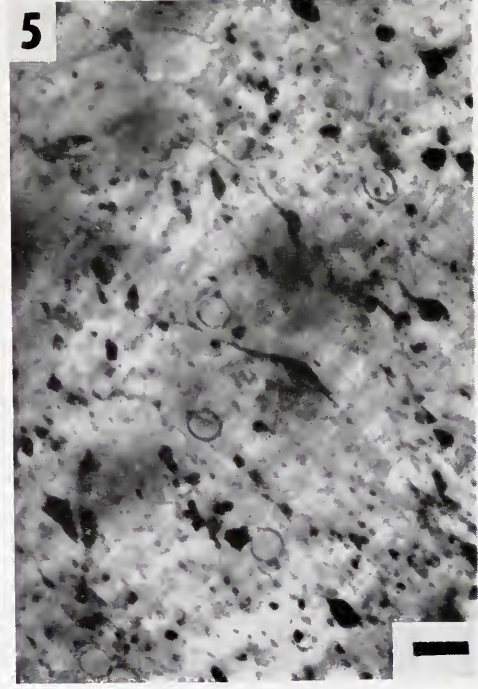
For studies on the effects of temperature on spontaneous electrical activity individual *Corymorpha* or their excised parts were placed in sea water on a sand bottom in an aluminum or glass container in a waterbath. Recordings were made from three intact animals, from three excised hydranths, and from six excised proximal tentacles from three different animals. Electrodes were placed in a variety of positions. The temperature of the waterbath was adjusted by adding ice or water of various temperatures and monitored by a thermistor probe, placed in the sea water next to the animal, with the output recording on one channel of the Dynograph. Temperature changes were made at several different rates.

## RESULTS

### *The structure of Corymorpha*

My morphological and histological investigations have generally confirmed the previous findings of Torrey (1902, 1904a, 1904b, 1905, 1907, 1910a, 1910b, 1910c) and Parker (1917). However, the results will be briefly summarized here since they are necessary for an adequate understanding of the experimental work.

Figure 1 shows some of the more significant anatomical features of *Corymorpha palma*. An undisturbed animal in its natural environment may reach a height of over 30 cm. Only the bottom fifth or less of the stalk is covered with perisarc. Frustules, or holdfasts, which anchor the stalk in the sand, grow out at the sides of each endodermal canal in the area covered with perisarc. As shown in Figure 1C, the axis of the stalk is filled with large endodermal cells, and the gastrovascular cavity has been reduced to canals which are spaced around the periphery of the stalk. From the exterior of the animal these canals are apparent as longitudinal white streaks which frequently anastomose, especially toward their proximal ends. The ectoderm of the stalk is made up of typical epitheliomuscular cells (Figs. 2, 3) with the muscle fibers running longitudinally next to the meso-





glea. Nematocysts are scattered among the epitheliomuscular cells and are more abundant on the naked distal part of the stalk.

The mesoglea forms a layer about 15  $\mu\text{m}$  thick (Chapman and Pardy, 1972), beneath which lie the endodermal cells. These cells occur in a continuum of sizes, from the small cells lining the canals to the very large cells which extend into the axis of the stalk. Those portions of the endodermal cells lying against the mesoglea contain muscle fibers which constitute the circular musculature of the stalk. The axial endodermal cells, which are remarkable for their great size, have only a thin rind of cytoplasm around a huge vacuole. A marked constriction separates the stalk from the hydranth.

The proboscis of *Corymorpha* is a complex structure with a basic musculature similar to that of the stalk, there being an ectodermal longitudinal layer and an endodermal circular layer. Groups of endodermal cells at the bases of the proximal tentacles partially separate the hydranth cavity into two chambers (Fig. 1B), the lower of which connects with the canals of the stalk.

Twenty to thirty large proximal tentacles arise at equal intervals around the base of the proboscis. Each tentacle is organized in a manner basically similar to the stalk: thin layers of ectoderm and mesoglea surround the large endodermal cells which fill the axis (Fig. 4). Torrey (1904a) described both circular and longitudinal muscles in both proximal and distal tentacles, but stated that the circular muscles form a much weaker sheet except where each tentacle joins the body of the hydranth. Parker (1917) and G. Chapman (personal communication) were unable to find any evidence for circular muscles.

A variable number of hollow stems which bear gonophores arises just distal to the proximal tentacles. The term "gonophore peduncles" will be used for these structures since, according to Hyman (1940), it is debatable whether they represent true blastostyles.

A bare zone above the gonophore peduncles is terminated distally by forty to sixty small distal tentacles which cover the sides of the proboscis and surround the mouth located at its tip. These tentacles are solid and are organized in the same manner as the proximal tentacles.

No previous investigators have noted the presence of nerves in *Corymorpha*, although Parker (1917, 1919) assumed that a nerve net is present. Methylene blue staining revealed what appear to be typical coelenterate nerve cells (Fig. 5) lying in the ectoderm above the mesoglea. However, only isolated cells stained; hence there was not clear evidence for a well-developed net or for concentrated nerve tracts.

---

FIGURE 2. Epitheliomuscular cells following maceration in Bela Haller's macerating fluid—microscope focused to show basal muscle fibers, Nomarski optics; Scale = 10  $\mu\text{m}$ .

FIGURE 3. Stalk ectoderm—a pavement epithelium formed by the upper part of the epitheliomuscular cells. Note nematocyst, Nomarski optics; scale = 10  $\mu\text{m}$ .

FIGURE 4. Large endodermal cells in proximal tentacles; scale = 10  $\mu\text{m}$ .

FIGURE 5. Methylene blue-stained nerve cells in the stalk of *Corymorpha*; scale = 10  $\mu\text{m}$ .

*Behavior of the whole animal*

In nature undisturbed *Corymorpha* are usually found standing relatively upright with the hydranth facing downstream when there is a current. At certain times of year the water of Newport Bay contains many strands of mucus from the gastropod, *Bulla*, and the proximal tentacles of *Corymorpha* may be festooned with these strands and the material trapped by them. From time to time one or more proximal tentacles will sweep inward carrying a small organism to the mouth or there may be some apparently random distal tentacle activity. In a few instances animals have been discovered with the mouth widely open and with the walls of the proboscis contracted longitudinally while a bolus of undigested material was regurgitated.

Concert and bowing behavior in *Corymorpha*, discussed in considerable detail

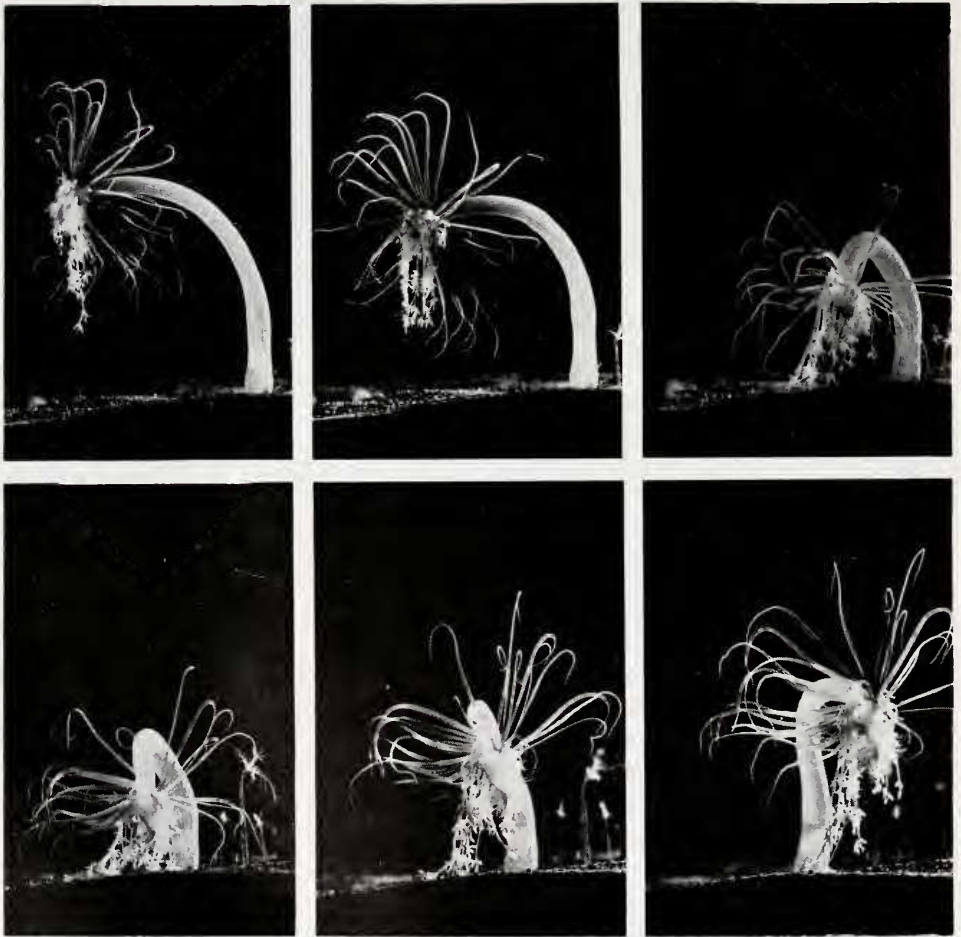


FIGURE 6. Bowing behavior in *Corymorpha*. Frames were taken at approximately 30-second interval and run from left to right, top to bottom.

by Parker (1917, 1919) appears to be limited to periods of quiet water; such periods are relatively short in the areas which I studied most thoroughly. Parker's observation on the inhibitory effect of a current was confirmed under field conditions by inversion of an aquarium over a portion of a bed of *Corymorpha*, all of which were standing erect in a current. Within a few minutes many of the animals under the aquarium began to show concert behavior and a variable degree of bowing, while their neighbors outside in the current continued to stand erect.

During concert behavior the proximal tentacles are simultaneously flexed inward around the proboscis from one to three times. Concurrently there is often a contraction of the stalk musculature. It appears that a majority of the polyps perform concert behavior sometime during any period of slack water. Some show this behavior quite regularly at intervals of 3-8 minutes, while others show no apparent rhythmicity.

Bowing behavior, if it occurs at all, normally occurs either simultaneously with stalk contraction or immediately thereafter. The bowing sequence shown in Figure 6 is atypical in that it did not start with stalk contraction and a concert. The degree to which an animal bows varies greatly from individual to individual. During the intervals when I was observing them, than 1% of the population bowed deeply enough to touch the distal tentacles to the substratum in the manner described by Parker (1917, 1919). Those animals which bowed deeply appeared to do so consistently.

The field and laboratory behavior which I have observed can be classified into individual acts and combinations of these acts such as:

1. Simultaneous outward and downward flaring of the distal tentacles, usually in response to some stimulus (distal opening response).
2. Longitudinal contraction of the proboscis.
3. Simultaneous inward flexion of all proximal tentacles.
4. Contraction of the longitudinal musculature of the stalk.
5. Bending of the stalk.
6. Peristaltic waves passing downward along the proboscis.
7. Inward movement of one or a few proximal tentacles.
8. Contraction of from one to many gonophore peduncles.
9. Bending of the proboscis to the side either spontaneously or in response to stimulation.
10. Apparently uncoordinated writhing or an oral flexion by some or all of the distal tentacles.
11. Opening and closing of the mouth.
12. Gaping of the mouth associated with regurgitation.

The list was still growing at the end of the study, so it should not be regarded as a complete enumeration of the acts of which *Corymorpha* is capable. Moreover, it is possible that some of the acts listed should be subdivided further. As it stands, however, the list summarizes the commonly observed behavior of *C. palma* and provides a way of discussing the individual acts which, together, encompass most of the behavior of the animal.

When possible the terminology established by Josephson and Mackie (1965) will be used whenever the behavior being described appears to be analogous to that

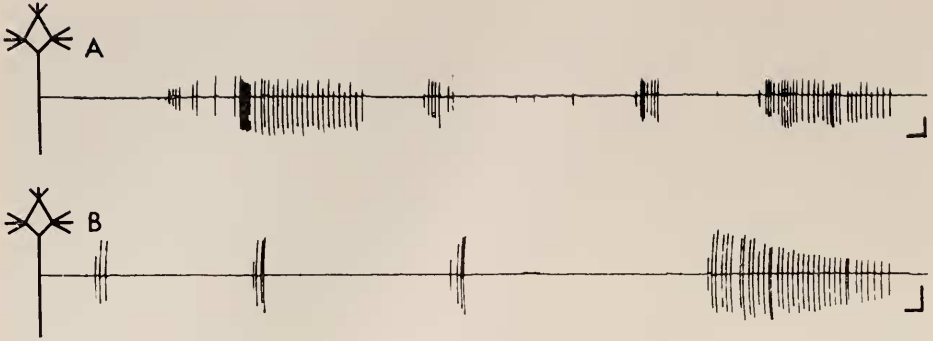


FIGURE 7. Stalk burst patterns in two *Corymorpha*. The approximate position of the recording electrodes is shown diagrammatically on the left; vertical scale equals  $500 \mu\text{V}$ ; horizontal equals 5 sec.

which they described in *Tubularia*. Following their usage, category (1) is termed a "distal opening response." Categories (2) and (3), which often occur in association with each other, constitute a "concert." A concert in conjunction with category (4) will be termed a "concert with stalk contraction." As previously noted, the degree of bowing varies greatly from individual to individual, so a "concert with stalk contraction" and a "concert with stalk contraction and bowing," category (5), must be regarded as the ends of a continuum with no clear separation between them. The other acts listed may occur independently and have not been given special names.

#### *Electrical activity and its behavioral correlates in the whole animal*

Following the usage set by Josephson and Mackie (1965) in *Tubularia*, the spontaneously active pulse systems in *Corymorpha* will be named according to the part of the animal in which the pulses appear to originate. Although "proboscis pulse" seems to be a more accurate term, the category "hydranth pulse" will be retained (a) because the pulses referred to under this title appear to be analogous in both *Tubularia* and *Corymorpha*, and (b) to avoid adding unnecessarily to the already extensive list of hydroid pulse types.

Pulse duration was measured from the initial departure from the recorded baseline to the final return to this baseline. Pulse amplitudes were measured from maximum negativity to maximum positivity. In all records negative potentials of the active electrode relative to the bath are displayed as downward deflections. The term "burst" is used in a rather broad sense to denote a temporally isolated series of two or more pulses. The number given in parentheses following each pulse category is a minimum estimate of the number of animals recorded from at that site.

*Stalk pulses (SP > 50).* Stalk pulses usually occur in bursts which may vary widely in duration and pulse number (Table I). Stalk burst patterns are shown in Figure 7. The site of initiation of stalk pulses varies from time to time and from animal to animal. Waveforms vary greatly both within and between animals



TABLE I

*Summary of Corymorpha stalk burst characteristics:  
each line represents a separate animal*

No. bursts measured	Range of burst durations (sec)	Av. burst duration (sec)	Range of SPs/burst	Av. no. SPs	Av. pulse frequency (SPs/sec)
1	8	8	4	4	0.50
3	5.2- 13.6	8.3	11-16	13.0	1.57
6	2.0- 45.0	14.8	4-35	13.8	0.93
9	2.0- 69.0	18.6	4-44	14.5	0.78
7	2.0-106.0	22.2	2-52	16.4	0.74
5	10.0- 50.9	27.4	14-45	27.6	1.01
2	48.0- 61.0	54.5	25-27	26.0	0.48
2	52.8- 58.0	55.4	33-43	38.0	0.69
4	51.0- 76.0	59.3	33-64	46.8	0.79
1	152	152	55	55	0.36
Av. 4	33.3- 64.0	42.1	18.5-38.5	25.5	0.79

at least when recording with suction electrodes. Characteristics of stalk pulses and other pulse types are summarized in Table II. The average conduction velocity based on a minimum of 18 measurements on each of 5 animals was 15.9 cm/sec (range of individual averages 14.9-18.2 cm/sec).

A contraction of the longitudinal muscles of the stalk almost always occurs simultaneously with a stalk burst; but one or two pulses sometimes occur without any apparent behavioral correlate. In general there is a clear association between the length of a burst and the strength of the associated contraction. Usually there is a concert associated with stalk bursts; but excision experiments clearly show that this is due to the triggering effect of the stalk activity.

Although pulses may be triggered by electrical stimulation at any point along the stalk, spontaneous bursts normally appear to originate in its lower half. To further examine sites of pulse initiation five stalks were cut into 3 approximately equal sections, each of which was found to be capable of generating spontaneous bursts. However, long bursts of 20 or more pulses were limited to the basal

TABLE II

*Summary of characteristics of the pulse types produced by Corymorpha. Average values were obtained by measuring 10 pulses from each of 5 animals. Distal tentacle pulses were measured on excised hydranths, all other types on intact animals*

Pulse type	Duration (msec)		Range of individual averages (msec)	Amplitude (mV)		Range of individual averages (mV)
	$\bar{X}$	S		$\bar{X}$	S	
Distal Tentacle Hydranth	63 ± 12		52-80	8.14 ± 5.23		3.78-15.95
Proximal Tentacle	68 ± 18		39-84	1.32 ± 0.84		0.34- 2.67
Gonophore Peduncle	89 ± 27		51-125	1.72 ± 1.77		0.61- 4.85
Stalk	75 ± 23		48-109	1.52 ± 0.58		0.74- 2.25
	61 ± 13		42-73	0.89 ± 0.35		0.49- 1.37

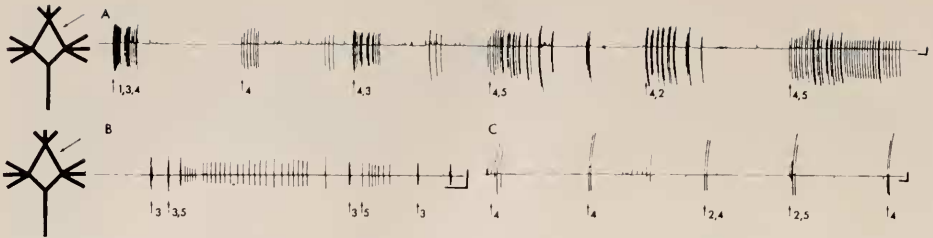


FIGURE 8. Types of hydranth pulse (HP) activity and associated behavioral correlates in *Corymorpha*. (A-C) Upward pointing arrows beneath the record indicate the point at which the behavior associated with the following numbers began: (1.) distal tentacles flare upward; (2.) distal tentacles flare downward; (3.) proximal tentacles simultaneously sweep inward around the proboscis; (4.) tip of the proboscis pulls downward; (5.) whole animal contracts. Vertical scale equals 1 mV; horizontal equals 5 sec.

segments of the stalks. Bursts of this length are often seen in intact stalks, again suggesting that pulses are normally triggered basally. The site of pulse initiation does sometimes shift within a burst (Fig. 10). *Corymorpha* does not have a distinct class of neck pulse as does *Tubularia*; but the stalk pulses of *Corymorpha* appear to have the same functional correlates as the neck pulses of *Tubularia*.

*Hydranth pulses (HP > 100)*. Hydranth pulses may occur alone, in pairs, or in bursts of varying length (Fig. 8). The most common pattern originating within the hydranth appears to be two to six pulses in quick succession at fairly regular intervals. (Fig. 8C). There are also many longer bursts originating either within the hydranth or the stalk (Fig. 8A, B). Waveforms vary greatly both within and between animals.

The behavioral correlates of hydranth pulses vary greatly from animal to animal. It is frequently difficult to discern any clearcut behavioral correlate of the commonly occurring regular pairs of pulses, although in some cases a wave of peristalsis passes down the proboscis and ends in a rather abrupt downward jerk of the proboscis coincident with each short burst of electrical activity. A complete behavioral response to a burst of hydranth pulses appears to be a simultaneous inward flexion of all proximal tentacles, associated with proboscis withdrawal but the observed response is frequently only some portion of this complete response. Thus, there may be a contraction with proximal tentacle flexion, or only some of the proximal tentacles may flex inward, or the proximal tentacles may flex inward only part way.

*Proximal tentacle pulses (PTP > 100)*. Each proximal tentacle has independent pacemakers that may generate pulses singly or in bursts. Frequently tentacle bursts are triggered by bursts of stalk or hydranth pulses, and when such triggering occurs the same burst pattern is usually recordable in all proximal tentacles along with occasional spontaneous activity. However, in other instances electrical activity in some or all of the tentacles may show no relation to that elsewhere in the animal.

It is likely that the site of PTP initiation varies from time to time and animal to animal. In most cases pulses recordable at the tip of a proximal tentacle and

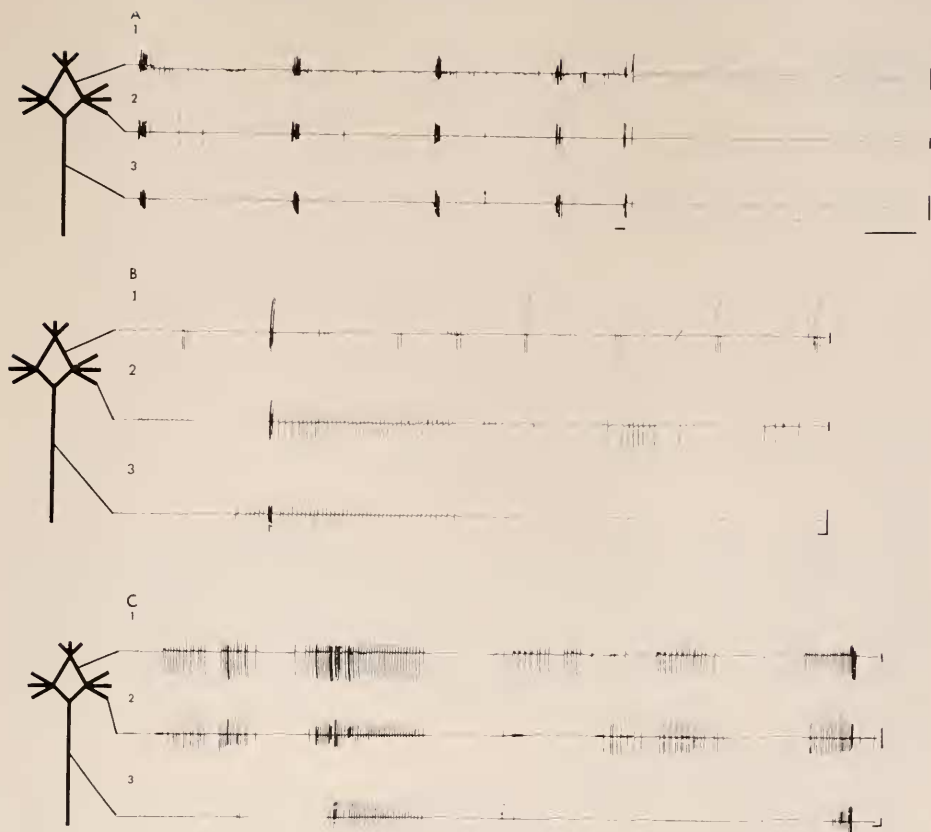


FIGURE 9. Relationships between electrical activity in the various pulse systems of *Corymorpha*. Vertical scale equals 1 mV; horizontal equals 5 sec, except that on the right in A which equals 0.1 sec.

not triggered from outside it fail to reach its base and are therefore not recorded in immediately adjacent proximal tentacles.

When recording from the whole animal there is often no apparent behavioral correlate of proximal tentacle pulses, although in some instances the tentacle is clearly flexing against the resistance of the electrode. This inactivity, however, appears to be an artifact of the recording conditions, since obvious flexions or contractions of the tentacles associated with electrical activity are observed in relatively less restricted isolated tentacles.

*Distal tentacle pulses* ( $DTP > 15$ ). Each distal tentacle has its own independent pacemaker, a fact readily apparent only after excision since there is little spontaneous electrical activity in attached tentacles. Distal tentacle pulses may occur singly or in bursts and usually follow activity in the proboscis. Therefore, the electrical activity in all distal tentacles is normally quite similar, in contrast to the situation in the proximal tentacles. There is no behavioral correlate of distal tentacle pulses recorded from the whole animal. As in the case of the proximal

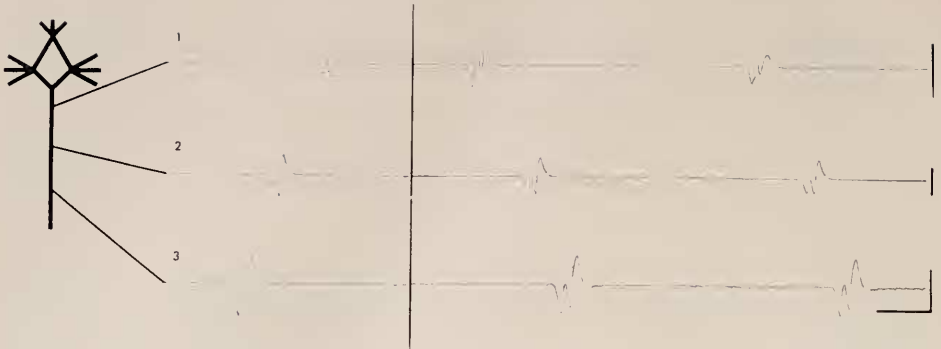


FIGURE 10. Lead shift during a burst. Pulses are consecutive. Vertical scale equals  $500 \mu\text{V}$ ; horizontal equals 0.1 sec.

tentacles, however, this appears to be an artifact caused by restriction by the electrode.

*Gonophore peduncle pulses* ( $GPP > 10$ ). Gonophore peduncle pulses may occur singly, but more often they occur as part of a burst, triggered from the proboscis. During a concert with stalk contraction it appears that the gonophore peduncles sometimes contract at about the same time as the proximal tentacles move inward around the hydranth. Spontaneous contraction of individual peduncles also occurs.

#### *Interactions between pulse systems*

Details of the interactions between spontaneous pulse systems are complex and somewhat variable, but certain valid generalizations can be made. Stalk bursts normally result in activity which can be recorded everywhere in the animal (Fig. 9A). During a stalk burst in an intact animal the bursts occurring both in the proximal tentacles and in the hydranth normally appear to be driven directly by stalk activity, but in some cases (Fig. 9B) only the proximal tentacles are driven. Proximal tentacle bursts are also often driven directly from the hydranth without stalk participation (Fig. 9C).

Since stalk bursts sometimes appear to be initiated by electrical activity in the hydranth the only generalization which appears to be valid is that a burst occurring

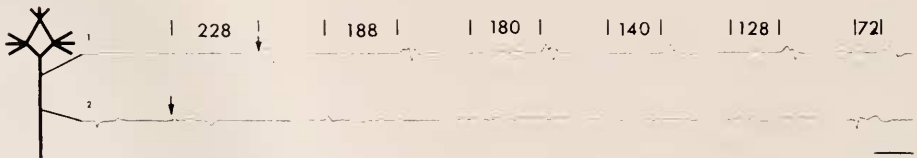


FIGURE 11. Evidence for a shifting pacemaker or for changing conduction velocity during a burst. The numbers above the record indicate the latency (msec) between the beginning of a single event as recorded at two places on the stalk. These intervals were measured as shown by the arrows associated with the first pulse. No vertical calibration was recorded.



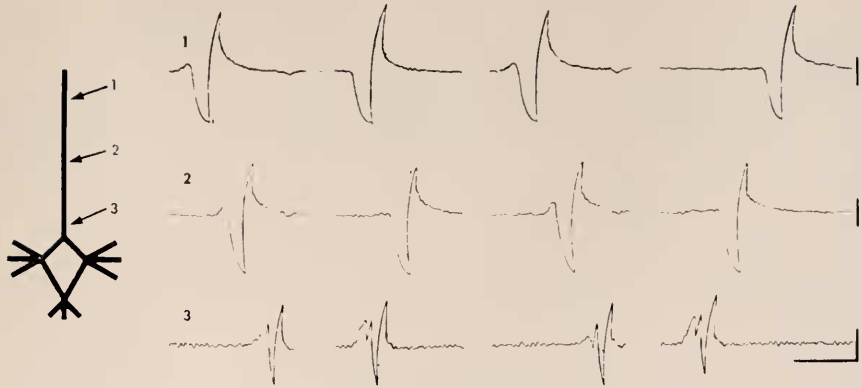


FIGURE 12. Records which can most easily be explained by hypothesizing simultaneous independent activation of more than one pacemaker. Vertical scale equals  $500 \mu\text{V}$ ; horizontal equals 0.1 sec. Sections were removed from the record (dotted lines) to allow reproduction.

in the stalk, regardless of its point of initiation, will usually also be recorded in the hydranth and proximal tentacles. In some cases the lead (triggering pulse) shifts back and forth between the hydranth and stalk or apparently between different parts of the stalk (Fig. 10), possibly indicating that the conducting system is unstable and can be triggered by small disturbances at many sites.

Successive pulses of a burst sometimes appear to show a marked change in velocity (Fig. 11). One alternative to an actual change in velocity is that several pulse initiation sites have been activated in different regions and are running independently of each other. Figure 12 shows a series of records which can apparently only be explained by hypothesizing independent activation of multiple sites of pulse initiation.

#### *Electrical activity and movement of isolated parts of Corymorpha*

In an isolated part electrical activity is often absent or at least reduced immediately following excision, but it usually returns within several minutes. Frequently there is a change in the pulse pattern. For example, the pulses may become more or less grouped into bursts; but it is impossible to attribute such changes unequivocally to excision. Figure 13A shows activity before and after the excision (a) of a proximal tentacle from the hydranth, then (b) of the hydranth from the stalk.

A much more direct correlation between electrical activity and movement is apparent in excised parts than in the whole animal. In most proximal tentacles there is nearly a one to one correlation between movements of the tentacles and single pulses, although sometimes there are pulses without obviously associated movements, and during bursts there may be a movement only on the first pulse. In distal tentacles movement appears to be correlated with each pulse, but many flexions lack apparent associated electrical activity. Excised proximal tentacles are capable of producing complex bursts (Fig. 13B, C) probably indicating simultaneous activation of more than one pacemaker. In excised gonophore peduncles most

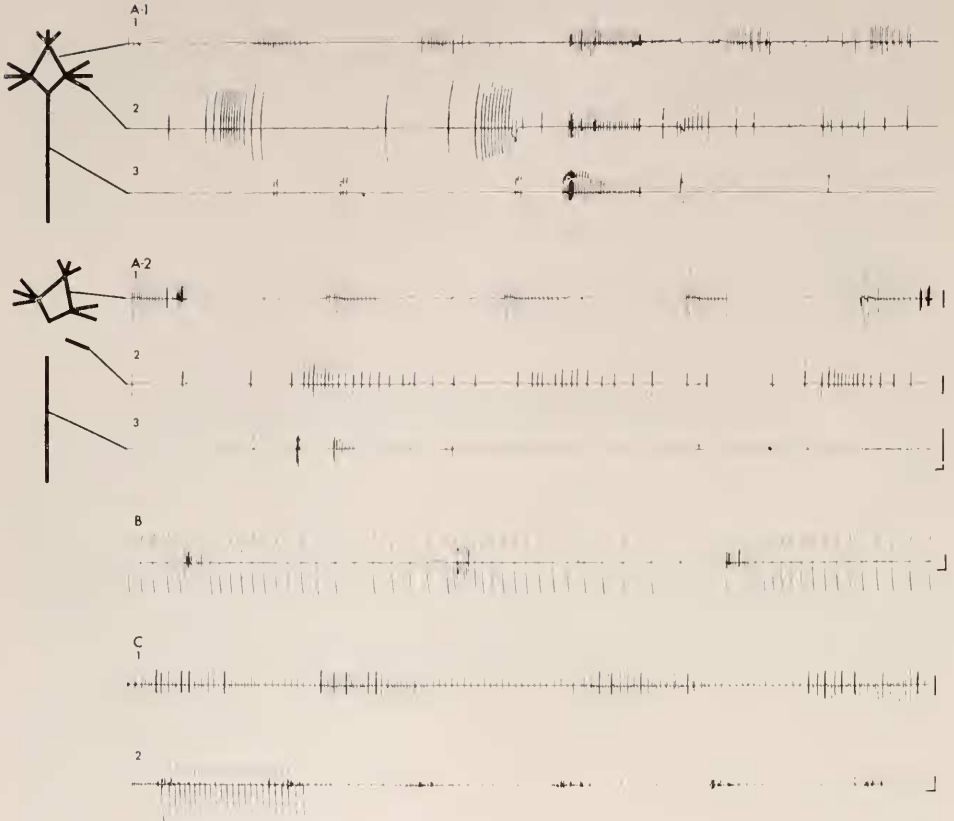


FIGURE 13. Excision experiments; (A.) electrical activity in various parts of a *Corymorpha* before (A-1) and after (A-2) their separation from the rest of the animal. (B.) An excised proximal tentacle is capable of producing bursts. (C.) More bursts produced by excised proximal tentacles. These records were made at 27° C. Records B and C2 are from the same tentacle. The excised proximal tentacle in A-2 was held by the tip; those in B and C were held by the cut basal ends. Vertical scale equals 2 mV; horizontal equals 5 sec.

activity appears to occur in bursts but there is no clear association between electrical activity and movement.

In excised hydranths the proximal tentacles continue to flare inward at the start of hydranth bursts, and the proboscis contracts during the burst if this behavior was initially present in the whole animal. Hydranth bursts often occur at quite regular intervals following excision, but not enough records were obtained to determine whether the apparent increase in regularity is significant. Isolated stalks contract either on the first pulse of a stalk burst or throughout the burst. Bursts of stalk pulses often come quite regularly.

In summary, excision experiments confirm the experiments on intact animals in indicating that there are at least five sets of pacemakers; namely, those in the stalk, hydranth, proximal tentacles, distal tentacles, and gonophore peduncles.

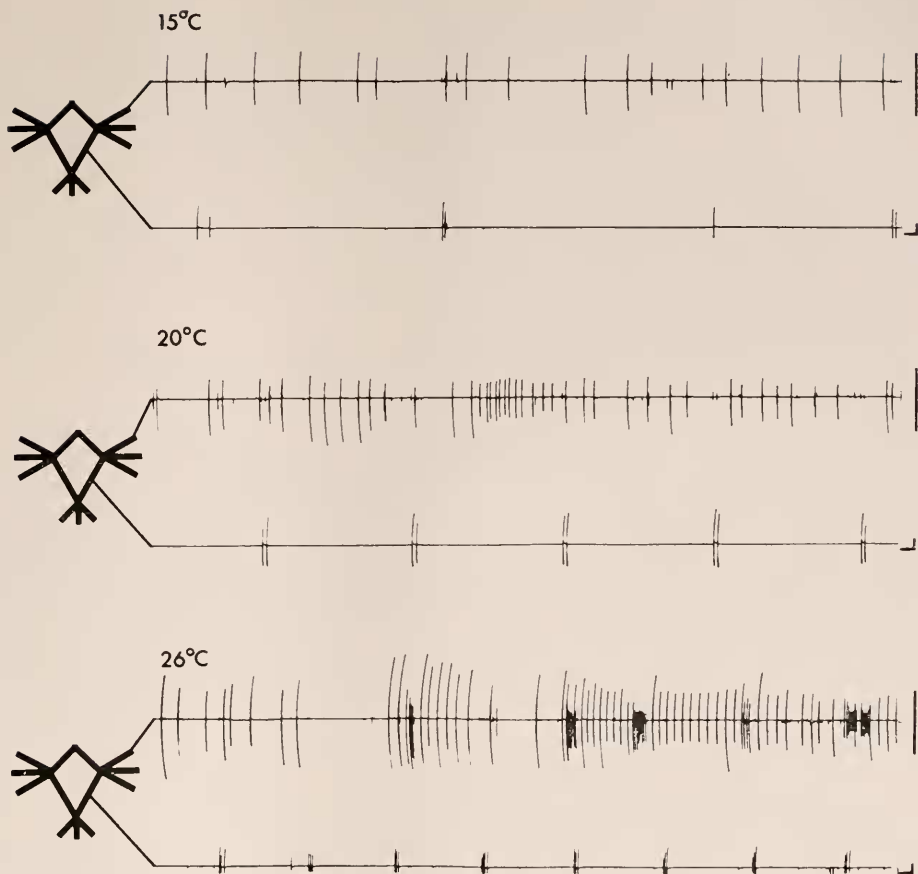


FIGURE 14. Effect of temperature on electrical activity in an excised hydranth of *Corymorpha*. All records are from the same hydranth. Temperatures are accurate to  $\pm 1^\circ$  C. Vertical scale equals 2 mV; horizontal scale equals 5 sec.

#### *Effects of temperature on spontaneous electrical activity*

Within the investigated range from 10 to  $30^\circ$  C pulse frequency increases with increasing temperature. Figure 14 shows the effect of temperature on electrical activity in a proximal tentacle and the proboscis of an excised hydranth. At temperatures in the neighborhood of  $28^\circ$  C animals sometimes generate a steady stream of high frequency pulses. Up to about this temperature the animals become more active, but beyond it they stand rather quietly. Pulse amplitude generally decreases below approximately  $15^\circ$  C and above about  $28^\circ$  C. Rapid temperature transitions, especially upwards, often cause an animal to become extremely active electrically.

#### DISCUSSION

As seen by comparison with the investigations of Josephson and Mackie (1965), the spontaneous pulse systems of *Tubularia* and *Corymorpha* are very much alike

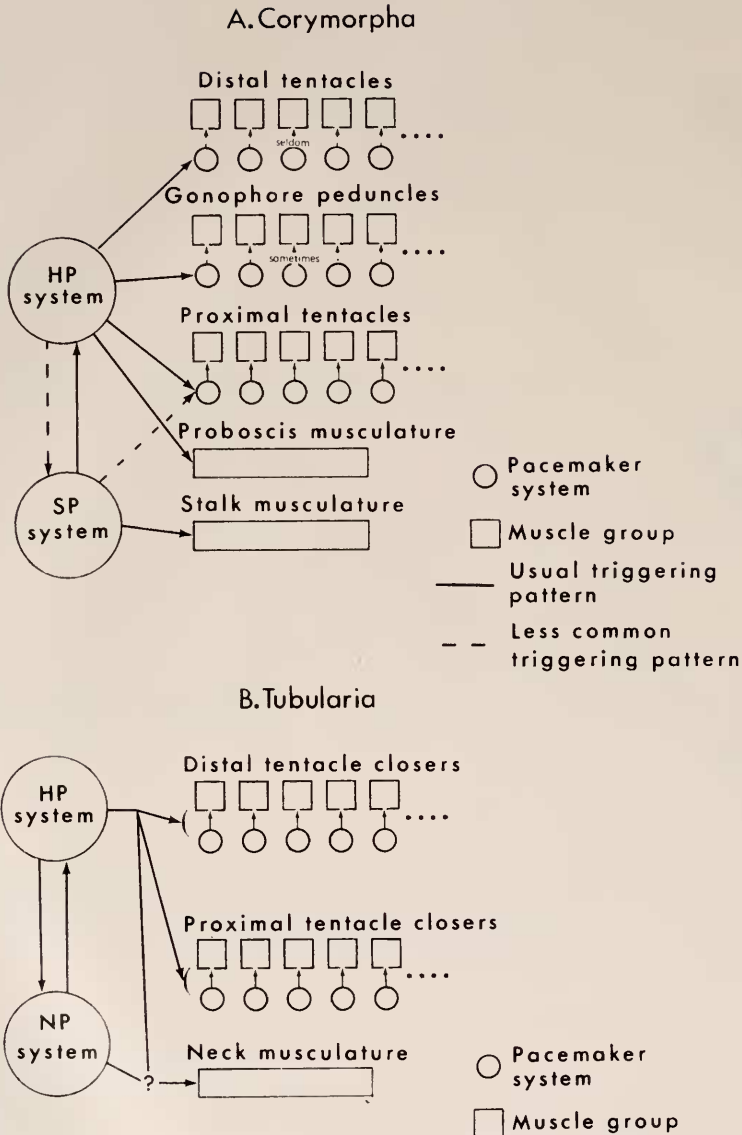


FIGURE 15. Comparison of interactions between pacemakers and effector systems in *Corymorpha* and *Tubularia*; (A.) *Corymorpha* (diagram modeled after that of Josephson and Mackie, 1965, for *Tubularia* which constitutes B of this figure), (B.) *Tubularia* (Josephson and Mackie, 1965).

in most respects. Pulse durations, waveforms, and amplitudes are all relatively similar in the two organisms. Stalk pulses in *Corymorpha* and neck pulses in *Tubularia* occur in relatively long bursts, although single pulse activity is quite rare in *Corymorpha* stalks and common in necks of *Tubularia*. Hydranth activity



in both animals often occurs in bursts of two to six pulses except when triggered by SPs (*Corymorpha*) or NPs (*Tubularia*). Proximal and distal tentacles and gonophore peduncles all have independent pacemakers although much of their electrical activity is triggered elsewhere in the animal. The pulse systems of both organisms are arranged in similar hierarchies (Fig. 15).

There are two significant differences between the spontaneous pulse systems of *Corymorpha* and *Tubularia* as they are diagrammed in Figure 15. First, proximal tentacle pulses are sometimes directly driven by stalk pulses in *Corymorpha*, but there is no indication that the NPs of *Tubularia* can perform a similar function. Secondly, the brackets enclosing both pacemakers and muscle groups in the distal tentacles of *Tubularia* indicate that the enclosed pacemakers and muscle groups are tightly coupled. In *Corymorpha* most hydranth pulse activity is recorded both in distal tentacles and in gonophore peduncles, but there is often no visible response associated with electrical activity in these structures.

There is considerable inter-individual variability in the relationship between electrical activity and behavior. This variability can be disconcerting, but after working with large numbers of either *Tubularia* or *Corymorpha* it becomes obvious that there is a general relationship, encompassing all individual variations, between electrical activity and behavior. For example, the extent of concert activity associated with hydranth pulses varies from an almost imperceptible contraction of the proboscis or a small inward flexion of the proximal tentacles to a violent, simultaneous oral movement of all the proximal tentacles associated with readily visible contraction of the proboscis. Concerts associated with stalk contraction are, in general, more vigorous than those initiated within the hydranth itself. There is also "loose coupling" (Josephson and Mackie, 1965) between stalk pulses and hydranth pulses, as exemplified by the failure of some stalk bursts to trigger concert behavior in some animals.

In contrast to this high degree of inter-individual variability the behavior of each animal is quite consistent. That is, once electrical activity and behavior of a given animal have been simultaneously observed for about 20 minutes, it usually becomes possible to describe the animal's behavior quite accurately from the electrical record alone.

Temperature has a marked effect on pulse generation frequency in *Corymorpha*, but, since the cellular elements responsible for this function have yet to be identified unequivocally the mechanism of this effect remains unknown. Rushforth (1971) and Rushforth and Burke (1971) have investigated pacemaker activity in *Hydra* and much of their discussions of pacemaker properties and possible models is also applicable to *Corymorpha*.

In *Corymorpha* the various pulse types are not distinguishable on the basis of waveform, amplitude, or duration. The average amplitude of distal tentacle pulses is considerably larger than that of other pulse types, but this is presumably an artifact of the much finer electrodes used to avoid entirely enveloping a distal tentacle. Also, it appears that all parts of the animal, with the possible exception of the perisarc-covered base of the stalk, are capable of pulse generation. Bearing this in mind, it might be argued that the pulse categories which have been set up are purely arbitrary. However, each of the five categories constitutes a demonstrable functional unit, which appears to be adequate justification for its establishment.

This account of the relation between electrical activity and behavior in *Corymorpha* leaves much complex behavior unexplained in terms of electrical activity. For instance, some distal tentacle movements and opening and closing of the mouth appear to occur without associated electrical activity, as does peristalsis of the proboscis, which is, however, often temporarily terminated by a contraction associated with hydranth pulses. Although the inhibition of concert and bowing behavior by a current suggests a sophisticated receptor-effector system, the elements of this system, and their mode of interaction, remain unknown. The same can be said of the mechanisms co-ordinating and controlling both regurgitation and the localized stalk contraction required to produce bowing. In general, the electrical activity which has been described here appears to be associated with contraction of the longitudinal musculature, although, as previously mentioned, there have been some animals and excised parts where such contraction was not visible.

Following Mackie's (1965) demonstration of epithelial conduction in siphonophores almost all investigators have regarded the relatively large spontaneous pulses which are recordable from many hydroids as being non-neural in origin. The main arguments supporting this hypothesis are the following: (1) the pulses are much too large and easily recordable with suction electrodes to originate in the fine neurons of the nerve net; (2) many types of pulses have a wide-spread distribution within the part of the animal where they occur; and (3) the duration of the pulses is greater than that of nerve impulses, with the possible exception of impulses in a few neurosecretory cells.

If the pulses recordable from *Corymorpha* are assumed to be nonneural, the role of the nervous system, the relation between electrical activity in the nervous system and that in the epithelial system, and any causal relationships between electrical activity in the two systems and behavior all remain to be elucidated. These relationships are considered in more detail in the following paper.

I thank Dr. James Case, Dr. James Morin and Dr. R. K. Josephson for helpful discussions during both research and writing and Dr. Larry Friesen for drawing Figure 1. The research was supported by an NDEA Title IV Predoctoral Fellowship and by PHS Grant NS 08599 to Dr. J. F. Case. This paper is based on part of a thesis presented to the Department of Biological Sciences, University of California, Santa Barbara, in partial fulfilment of the requirements for the Ph.D.

#### SUMMARY

1. There is a clear association between certain aspects of the behavior of *Corymorpha palma* and electrical activity of five interacting pulse systems located in the stalk, hydranth, proximal tentacles, distal tentacles, and gonophore peduncles.

2. Stalk pulses normally occur in bursts of 10 to 30, and are associated with contraction of the longitudinal musculature of the stalk. They apparently may originate anywhere on the stalk, but are usually initiated in its basal half.

3. Hydranth pulses occur in bursts of varying lengths, the most common consisting of 2-6 pulses. These pulses are associated with a "concert" which varies greatly in intensity from animal to animal. A full concert involves contraction of the proboscis as the proximal tentacles come in around it, though some animals show nothing more than a twitch of the proximal tentacles or a barely perceptible contraction of the proboscis.

4. Proximal and distal tentacle pulses may occur singly or in bursts which are usually triggered from outside the tentacle. While the tentacle is attached to the animal there is sometimes no obvious behavioral correlate of these pulses; but with excised tentacles there is usually a flexion or slight contraction associated with each pulse or burst of pulses.

5. Gonophore peduncle pulses may occur singly or in bursts which are usually triggered from outside the peduncle. In some cases there is no obvious behavioral response to these pulses, while in others there is a contraction of the ectodermal musculature.

6. The pulse systems are arranged in a coupled hierarchy with stalk bursts normally triggering activity everywhere else in the animal, either directly or by way of the hydranth pulse system. This triggering results in concerts associated with stalk contraction; such concerts occur either irregularly or at fairly regular intervals of several minutes in undisturbed animals. Hydranth pulses trigger pulses in both sets of tentacles, resulting in concerts. Excision experiments were used to clarify these relationships between the various pulse systems.

7. Temperature has a marked effect on pulse activity. Proximal tentacle pulses and hydranth pulses are much more frequent at high temperatures and are less frequent at low temperatures over the range 10–30° C.

8. The spontaneous pulse systems of *Tubularia* and *Corymorpha* are similar in many respects.

9. The pulse systems of *Corymorpha* cannot be differentiated on the basis of pulse duration, amplitude, or waveform.

10. Much of the more complex behavior of *Corymorpha* cannot be explained in terms of recordable electrical activity. The mechanisms by which this behavior is controlled remain unknown.

#### LITERATURE CITED

- CHAPMAN, G., AND R. L. PARDY., 1972. The movement of glucose and glycine through the tissues of *Corymorpha palma* Torrey (Coelenterata, Hydrozoa). *J. Exp. Biol.*, **56**: 639–645.
- GATENBY, J. B., AND T. S. PAINTER, 1937. *The Microtometist's Vade-Mecum: A Handbook of the Methods of Animal and Plant Microscopic Anatomy*. Blakiston, Philadelphia, 784 pp.
- HYMAN, L. H., 1940. *The Invertebrates: Protozoa through Ctenophora*. McGraw-Hill, New York, 726 pp.
- JOSEPHSON, R. K., 1961a. Colonial responses of hydroid polyps. *J. Exp. Biol.*, **38**: 559–577.
- JOSEPHSON, R. K., 1961b. Repetitive potentials following brief electrical stimuli in a hydroid. *J. Exp. Biol.*, **38**: 579–593.
- JOSEPHSON, R. K., AND G. O. MACKIE, 1965. Multiple pacemakers and the behaviour of the hydroid *Tubularia*. *J. Exp. Biol.*, **43**: 293–332.
- JOSEPHSON, R. K., AND J. UHRICH, 1969. Inhibition of pacemaker systems in the hydroid *Tubularia*. *J. Exp. Biol.*, **50**: 1–14.
- MACKIE, G. O., 1965. Conduction in the nerve-free epithelia of siphonophores. *Amer. Zool.*, **5**: 439–453.
- MACKIE, G. O., 1968. Electrical activity in the hydroid *Cordylophora*. *J. Exp. Biol.*, **49**: 387–400.
- MORIN, J. G., AND I. M. COOKE, 1971a. Behavioural physiology of the colonial hydroid *Obelia*. I. Spontaneous movements and correlated electrical activity. *J. Exp. Biol.*, **54**: 689–706.
- MORIN, J. G., AND I. M. COOKE, 1971b. Behavioural physiology of the colonial hydroid *Obelia*.

- II. Stimulus-initiated electrical activity and bioluminescence. *J. Exp. Biol.*, **54**: 707-721.
- PARKER, G. H., 1917. The activities of *Corymorpha*. *J. Exp. Zool.*, **24**: 303-331.
- PARKER, G. H., 1919. *The Elementary Nervous System*. J. B. Lippincott, Philadelphia, 299 pp.
- P'ARMENTIER, J., AND J. CASE, 1973. Pharmacological studies of coupling between electrical activity and behaviour in the hydroid. *Tubularia crocea* (Agassiz). *Comp. Gen. Pharmacol.*, **4**: 11-17.
- PASSANO, L. M., AND C. B. McCULLOUGH, 1962. The light response and rhythmic potentials of *Hydra*. *Proc. Nat. Acad. Sci.*, **48**: 1376-1382.
- PASSANO, L. M., AND C. B. McCULLOUGH, 1963. Pacemaker hierarchies controlling the behaviour of hydras. *Nature*, **199**: 1174-1175.
- PASSANO, L. M., AND C. B. McCULLOUGH, 1964. Coordinating systems and behaviour in *Hydra*. I. Pacemaker system of the periodic contractions. *J. Exp. Biol.*, **41**: 643-664.
- PASSANO, L. M., AND C. B. McCULLOUGH, 1965. Coordinating systems and behaviour in *Hydra*. II. The rhythmic potential system. *J. Exp. Biol.*, **42**: 205-231.
- RUSHFORTH, N. B., 1971. Behavioral and electrophysiological studies of *Hydra*. I. Analysis of contraction pulse patterns. *Biol. Bull.*, **140**: 255-273.
- RUSHFORTH, N. B., AND D. S. BURKE, 1971. Behavioral and electrophysiological studies of *Hydra*. II. Pacemaker activity of isolated tentacles. *Biol. Bull.*, **140**: 502-519.
- TORREY, H. B., 1902. The hydroids of the Pacific Coast of North America. *Univ. Calif. Publ. Zool.*, **1**: 1-104.
- TORREY, H. B., 1904a. Biological studies on *Corymorpha*. I. *C. palma* and environment. *J. Exp. Zool.*, **1**: 395-422.
- TORREY, H. B., 1904b. The hydroids of the San Diego Region. *Univ. Calif. Publ. Zool.*, **2**: 1-43.
- TORREY, H. B., 1905. The behavior of *Corymorpha*. *Univ. Calif. Publ. Zool.*, **2**: 333-340.
- TORREY, H. B., 1907. Biological studies on *Corymorpha*. II. The development of *C. palma* from the egg. *Univ. Calif. Publ. Zool.*, **4**: 253-298.
- TORREY, H. B., 1910a. Biological studies on *Corymorpha*. III. Regeneration of hydranth and holdfast. *Univ. Calif. Publ. Zool.*, **6**: 205-221.
- TORREY, H. B., 1910b. Note on geotropism in *Corymorpha*. *Univ. Calif. Publ. Zool.*, **6**: 223-224.
- TORREY, H. B., 1910c. Biological studies on *Corymorpha*. IV. Budding and fission in heteromorphic pieces and the control of polarity. *Biol. Bull.*, **19**: 280-301.